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The Production of Meiofauna.

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Introduction.

The productivity of aquatic populations has received much attention since the International Biological Programme during which several books appeared that much influenced later developments. Among the standard works in the field one needs to mention Edmondson & Winberg (1971), Holme & McIntyre (1971, 1984), Winberg (1971), Zaika (1973). One of the important consequences was the standardization of concepts and symbols and the acquisition of a large body of data which had its theoretical roots in the paradigm of trophic organisation of ecosystems developed by Lindeman (1942).

In steady state conditions the energy budget of an organism may be described by the well known equation:

$$C = P + R + F + U$$

where C is food intake or consumption, P is production of biomass, R is respiration, F is egested faeces and U is excretion. Production is the sum of somatic growth and reproductive output $P = P_g + P_r$. Absoption (Ab) is the portion of the consumption not egested as faeces $Ab = C - F = P + R + U$. Assimilation (A) is the portion of consumed energy used for production and respiration $A = P + R$.

In this equation all variables have to be expressed in the same units, e.g. $kJ.m^{-2}.an^{-1}$. One has to be aware that even then the ecological meaning of each term is quite different: growth and reproduction yield high energy particulate organic matter, respiration has as its end product CO_2, a gaz, faeces is low-energy particulate matter and many excretion products are soluble and may be organic or inorganic. In order to evaluate their pathways in the ecosystem the redox-potential of these end-products may be a useful parameter.

2. Production

Production measures the part of the energy consumed by a population that is transformed into organic matter (body tissues and reproductive products) potentially available for consumption by populations from a higher trophic level. Gross and net growth efficiencies of animals (K_1 and K_2) and production efficiency $P/A = P/(P+R)$ of populations may be relatively predictable, and are therefore worth studying.

2.1. Somatic growth.

Production by somatic growth is the sum of the growth increments of all individuals in the population during a certain time, including the growth of the individuals that died during the interval. The methods used to measure production depend on the life history of the population. These methods can be reduced to two types: summation of eliminated biomass or summation of growth increments. According to the method used one needs good data either about growth, reproduction and recruitment or about mortality and changes in biomass.

The equivalence between both approaches has been demonstrated by Crisp (1971). In the first case growth processes can be ignored if the biomass eliminated during the time period Δt considered can be accounted for:

$$P = B_1 - B_0 + M$$

where M is the eliminated biomass during Δt.

When the finite mortality rate $\Delta N/\Delta t$ of individuals from weight class i (mean weight $\bar{w}_i$) is Z_i then the expected mortality during Δt is $Z_i\ \Delta t$ and the expected loss of biomass is $Z_i w_i\ \Delta t$. Thus :

$$M = \Sigma_i\ Z_i \bar{w}_i\ \Delta t$$

and

$$P = \Delta B + \Sigma_i\ Z_i \bar{w}_i\ \Delta t \qquad (1)$$

In the second case production is measured as the sum of the growth increments of all individuals in the population during Δt:

$$P = \Sigma_i\ N_i G_i w_i\ \Delta t \qquad (2)$$

where G_i is the instantaneous weight specific growth rate

$$G_i = \frac{1}{w_i} \frac{dw_i}{dt}$$

and N_i is the mean number of individuals alive in weight class i during the interval.

In both equations (1) and (2) growth and mortality have to be known as a function of individual weight. Using (1) one needs to know weight-specific mortality, using (2) one needs to know weight-specific growth.

Cohort populations.

If cohorts (same-aged individuals) are recognizable as a result of semi-simultaneous reproduction, production measurement is relatively easy if emigration an immigration can be accounted for. The methods require accurate estimates of abundance and weight over time. Four basic and equivalent methods exist (Waters & Crawford, 1973 ; Heip et al., 1982a) :

- increment-summation : production during a time interval is the product of the average abundance on two successive dates and the change in average weight of an individual :

$$P = \Sigma_i \, \overline{N_i} \, (\Delta w)_i$$

- removal-summation : production during a time interval is calculated as the change in abundance multiplied by the average individual weigth during the interval :

$$P = B_2 - B_1 + \Sigma_i \, (-\Delta N)_i \, \overline{w_i}$$

- instantaneous growth : the average biomass in a sampling interval is multiplied by the instantaneous weight-specific growth rate (assumed constant during the interval) :

$$P = \Sigma_i \, G_i \, \overline{B_i}$$

- Allen curve : mean weight is plotted against abundance (survivorship) and production is the surface under the curve.

Non-cohort populations.

When cohorts are not identifiable, as is the case for most meiofauna populations, due to overlapping generations or continuous reproduction, methods to calculate production require data on incremental increases in weight of individuals from the time they are born until they die. Most methods are based on knowledge of the finite growth rate of an individual over its life. Growth increment methods use experimental growth curves or estimations of stage durations, elimination methods include the size-frequency method and population dynamical models.

The size frequency method was originally designed for estimation of the correct order of magnitude of production by Hynes (1961) and subsequently refined (Hynes & Coleman, 1968; Benke, 1979). Thereby the method was restricted to the analysis of species groups with similar generation times, size and trophic position. The population is divided into size classes of similar duration. It was adapted to, and used for, populations divided in developmental stages by Herman et al. (1983, 1984a) and Herman & Heip (1985).

Estimations of the duration of life stages in the population can be obtained from laboratory experiments or from population models fitted to the field data. Laboratory experiments offer the possibility to establish complete life and fertility tables (e.g. Vranken & Heip, 1983). However, they pose the problem of extrapolating the results to the field.

Fitting models to field data (e.g. the methods of estimating birth and death rates or stage-frequency methods) requires additional data or assumptions on the population. Stage-frequency methods are extensively reviewed by Southwood (1978). Threlkeld (1979) gives an example of estimating birth and death rates by using extra information on the age distribution of Daphnia embryos. Herman et al. (1983) estimate the duration of developmental stages in the ostracod Cyprideis torosa by counting empty shells in the sediment : the distribution of the empty shells over the stages gives information about the mortality in the different stages.

2.2 Reproductive output.

Reproductive output may make up a considerable part of the total production of a population. In three populations of meiobenthic copepods it was estimated as between 13 and 29 % of the total production (Feller, 1982, Herman & Heip, 1985).

Values for nematodes in lab cultures range from 10 % (Warwick, 1981) to over 90 % (Schiemer, 1983). These values strongly depend on the culturing conditions (Vranken & Heip 1983, 1986; Vranken et al. in press).

Apart from the experimental conditions, the age structure of the population is important in determining the relative importance of reproductive output. If the population is in stable age distribution at exponential growth, it will mainly be composed of fast-growing juveniles.

However, if juvenile mortality is important the population age structure will be different and the relative importance of egg production may well increase. This is most probably the case in the above-mentioned copepod populations, where naupliar mortality rates are much larger than copepodite and adult mortality rates (this does not prevent that naupliar production was quite important : naupliar and egg production together accounted for 54-55 % of the total production in all three studies mentioned).

Meiofauna production.

In practice it is often impossible to use any of the described methods for meiofaunal populations. Direct production estimates of field populations only exist for a few species : four harpacticoid species (Feller, 1982; Fleeger & Palmer, 1982; Herman et al. 1984a; Herman & Heip, 1985), and an ostracod species (Herman et al., 1983).

Laboratory experiments pose their own problems. Many species of nematodes and copepods have now been cultured (see reviews by Heip et al., 1985 and Hicks & Coull, 1982). Two trends seem clear. In setting up experiments, one almost automatically selects the more "weedy" species. It is no wonder that so many data are available on the genera Monhystera (for nematodes) or Tisbe (copepods). Second, the more one knows about a species, the clearer become the effects of the culture conditions. As an example, Vranken et al. (in press) show that for Monhystera disjuncta, cultured with different bacterial strains as food and with different densities of one strain, the minimum generation time can differ with a factor 1.4, whereas the egg production rate differs with a factor 3.5.

In view of the gross uncertainties introduced using laboratory experiments, indirect approaches have been advocated. The following are to be mentioned :

- **Measurement of respiration.** When a proportionality between production and respiration of a population is assumed, respiration measurements may be used to estimate production, though respiration measurements also are technically difficult for meiofauna. Humphreys (1979) showed a significant log-log relationship between population production and population respiration whith a slope equal to one, which implies that P/(P+R) is independent of size. This study covered populations from widely different ecological and taxonomical groups, but no meiofauna. Herman et al. (1984b) were able to compare respiration and field production of three meiofaunal populations (one ostracod and two harpacticoid copepods) and found indeed a constant value $P/(P+R) \approx 0.4$.

For nematodes, Schiemer et al. (1980), Tietjen (1980), Warwick (1981) and Schiemer (1982a,b) found much higher values, in the order of 60-90 %. Herman et al. (1984b) discuss some of the factors possibly responsible for such a large difference. However, Herman & Vranken (submitted) also found very high production efficiencies (> 60 %) for a cultured population of Monhystera disjuncta, even when factors such as the "negative production" (due to weight loss) in the egg stage is taken into account. High production efficiencies seem to be a consistent feature of nematode populations.

Are nematodes so much more efficient than e.g. copepods, converting up to 90 % of their energy intake into production ? At the moment, this cannot be excluded, although it seems improbable. An interesting alternative hypothesis is that respiration measurements underestimate the energy losses. Microelectrode measurements show that in many sediments no free oxygen is present from a depth of a few mm onwards (see e.g. Revsbech et al., 1980). In these sediments one can easily find nematodes down to a depth of...10 cm. This is also true in sediments without animal burrows, which have been advocated to be a major source of oxygen to the meiofauna (Reise & Ax, 1979). It is almost inevitable to conclude that most nematodes live (at least partially) anaerobically. It is possible that even in the presence of oxygen, where they do have a measurable respiration, they do not use fully aerobic metabolic pathways. This is a field of research which surely provides the scope for interesting studies. In the meantime, the estimation of production based on respiration becomes quite questionable. At least it seems safest to assume a very high "apparent production efficiency" for nematodes.

When the problem of production efficiencies could be solved, the estimation of production from respiration has some practical advantages. Warwick & Price (1979) showed that, after correction for temperature, the community respiration of nematodes nearly equalled 6 l O_2 g^{-1} wwt an^{-1} in several habitats, where individual nematode weight differed by an order of magnitude.

- P/B ratios and body weight: Gerlach (1971) provided the first estimate of annual P/B = 9 for meiofauna in general. The figure has two components, a life cycle turnover of three and three generations annually. The justification for the first assumption lies in a model study by Waters (1969) who showed that for a wide variety of growth and mortality models, the lifetime P/B does not vary greatly around a modal value of 3.5. Herman et al. (1984b) showed that for nematodes under certain conditions (neonate weight is production, juvenile growth is exponential, adult growth is not too important and the generation time is defined as the development time of juveniles) a P/B = 3 per generation (juvenile period) may be expected.

Scaling of annual P/B to body size has been proposed by Banse & Mosher (1980), who showed a log-log relationship between the two variables. It was applied to meiofauna by Heip et al. (1982a) and to nematodes by Vranken & Heip (1986). Both compilations of meiofauna data show that the weight dependence coefficient in meiofauna is similar to the general value found by Banse & Mosher (1980). However, the intercept values are much lower, in the order of 1/10 the intercept values of the macrofauna. This feature was anticipated by Banse & Mosher (1980), and discussed by Heip et al. (1982a) and Vranken & Heip (1986). However, no conclusive arguments have been found to explain it.

- The number of generations : since the P/B per generation (juvenile developmental period) is around three a fairly accurate indirect estimation of production may be obtained by multiplying the number of generations produced annually by this figure. The reviews of Heip et al. (1982b, 1985) and Hicks & Coull (1982) give data on the annual number of generations in nematodes and copepods respectively. For both these groups it is clear that a uniform value for the number of generations produced annually does not exist and that each population has to be studied in its own right.

For nematodes the existing data from lab cultures have been reviewed by Vranken et al. (1986) who proposed the following equation relating the egg to egg development time T_{min} to temperature and adult female weight W :

$$\log T_{min} = 2.202 - 0.0461\ t + 0.627 \log W$$

When multiplied by the constant biomass turnover per generation $(P/B)_g$ = 3, development rate $1/T_{min}$ can be used as a predictor of daily P/B. This estimate is as representative for the nematode community as the cultured species are. The danger thus exists that the estimate, based on "weed" species, gives an overestimate of the real production. However, some comforting evidence regarding its usefulness was presented by Vranken et al. (1986).

Production and Biomass of meiofauna in the North Sea.

Energy flow models for the North Sea use meiobenthic biomass to evaluate the trophic role of the meiofauna. Usually, the biomass (around 1-2 g dwt m^{-2} for subtidal sediments) is multiplied by a constant factor (often 8-10) to obtain a production of 8-20 g dwt m^{-2} an^{-1} and energy consumption, which is perhaps around five times this value, i.e. 40-100 g dwt m^{-2} an^{-1}, or 16-60 g C m^{-2} an^{-1}. Gross uncertainties are present in such extrapolations and the use of a single P/B ratio has been strongly discouraged by Vranken & Heip (1986).

The reasonably constant production efficiency P/A $\approx$ 0.4 found in "aerobic" meiofauna poplations may be used to obtain estimates of production from respiration measurements. In order to evaluate the energy consumption of a population one may try to obtain similar constants for P/C. Very few data exist on which such extrapolations might be based. Heip et al. (1985) summarize the data for nematodes. Consumption of bacteria and algae by three species of nematodes varied between 14 and 60.10^{-2} µg C d^{-1}. Admiraal et al. (1983) estimated that a nematode eats about double its own carbon content each day. A community with a standing stock of 0.3 g C m^{-2} would then consume about 220 g C m^{-2} an^{-1}. However, it is unreasonable to extrapolate the (spring) rates from a highly productive intertidal community to subtidal communities without <u>in situ</u> primary production.

The evaluation of nematode production given by Heip et al. (1982a) and Heip et al. (1984) for areas in the Southern Bight have been revised by Heip et al. (1985). Two constrasting situations were compared. On a linear sandbank with little organic input nematode biomass was 0.07 g C m^{-2}. Nematode respiration was calculated as 1.06 g C m^{-2} an^{-1}. If production efficiency is 40 %, nematode production then would be 0.71 g C m^{-2} an^{-1} and with an assimilation efficiency of 20 %, consumption would amount to 8.8 g C m^{-2} an^{-1}. However, with a production efficiency of 70 %, total consumption would be 17.7 g C m^{-2} an^{-1}. In the first case P/B per year would be 10.1, in the second case it would be 35.3.

Use of the P/B - body weight relation necessitates the knowledge of the distribution of adult sizes of the species in the community. A gross

estimate, taking an average female size of 0.4 µg dwt (average individual size is 0.26 µg dwt), results in a yearly P/B of 16.6, using the equation given by Vranken & Heip (1986). This is in between the two previous estimates. It is near to the annual P/B of 20 estimated by Vranken et al. (1986) for an impoverished sublittoral nematode community in the North Sea.

It is at least as difficult to estimate the production of the harpacticoid copepods in the North Sea. A very rough guess could proceed as follows. We assume an average biomass of 20 µg dwt / 10 cm^2: this is based on the observation that when density is high, individual weight is low, thus compensating for the higher numbers. We further assume an average respiration rate of 3 nl O_2 h^{-1} (µg dwt)$^{-1}$. This is in the lower end of the range described by Herman & Heip (1983), and in the same order as found by Gee & Warwick (1984) for interstitial species. Respiration would then amount to 0.21 gC m^{-2} an^{-1}. With a production efficiency of 0.4, production is 0.14 gC m^{-2} an^{-1}. With an assimilation efficiency of 20 %, total consumption would thus amount to 1.75 gC m^{-2} an^{-1}. Annual P/B would equal around 14.

It should be stressed that these estimates are not much more than guesses. They show that consumption by meiofauna is in the order of 10 gC m^{-2} an^{-1}. Nematodes are almost an order of magnitude more important than harpacticoids.

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